

RESOURCE PARTITIONING OF SPIDER HOSTS (ARACHNIDA, ARANEAE) BY TWO MANTISPID SPECIES (NEUROPTERA, MANTISPIDAE) IN AN ILLINOIS WOODLAND

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ABSTRACT. Two spider-boarding mantispids, *Mantispa uhleri* Banks 1943 and *Climaciella brunnea* (Say 1824), were found to be partitioning available spider egg resources in an Illinois woods based on vertical stratification. *Mantispa uhleri* was found to be phoretic on the philodromid *Philodromus vulgaris* (Hentz 1847), the salticid *Metacyrba undata* (De Geer 1867) and the anyphaenid *Aysha gracilis* (Hentz 1847) at levels of 75%, 26%, and 27% respectively. All of these spiders were collected from areas above the forest floor. In contrast, *C. brunnea* was collected from 19% of leaf litter-inhabiting lycosids of the genus *Schizocosa*. There was no host range overlap within the woods, but in a grassy field without appreciable stratification of vegetation adjacent to the woods, both *M. uhleri* and *C. brunnea* were found aboard the lycosid *Rabidosa punctulata* (Walckenaer 1837) at levels of 2% and 7% respectively. A single larva of *Mantispa pulchella* (Banks 1912) associated with an anyphaenid from the woodland sample was also collected in this study. Mantispids are far more common than has been previously supposed and are likely an important factor in spider population dynamics and the evolution of spider behavior.

Keywords: *Mantispa uhleri*, *Climaciella brunnea*, *Mantispa pulchella*

The neuropteran family Mantispidae, subfamily Mantispinae, contains insects whose larvae are spider-egg predators (Redborg 1998). Larvae obtain eggs in one of two ways: (1) direct penetration of an egg sac by first instar larvae that search for egg sacs in the field, or (2) boarding adult female spiders and entering the spider's egg sac while it is being constructed (Redborg & MacLeod 1985). Inside the egg sac, larvae pierce and drain the eggs with a sucking tube formed by modified mandibles and maxillae. After three larval instars, the developing mantispid spins a cocoon inside the egg sac using silk from the Malpighian tubules.

The species of spiders utilized by mantispids in North America are partially known for a number of species including *Mantispa uhleri* Banks 1943 (Redborg & MacLeod 1985), *Mantispa fuscicornis* Banks 1912 from Texas (Rice 1986; Rice & Peck 1991, cited as *Mantispa sayi* Banks 1897) and *Mantispa pulchella* (Banks 1912) (Hoffman & Brushwein 1989), *Mantispa interrupta* Say 1825 (Hoffman & Brushwein 1990) and *Mantispa viridis* Walker 1853 (Brushwein et al. 1992) from South Carolina. Much of this work has not been quantitative. Moreover, little is known

about how sympatric mantispids interact in their selection of hosts. Here we report on the resource use of two mantispid species in Illinois.

The present study developed while we were collecting overwintering larvae of *M. uhleri* for a laboratory experiment from two of its host spiders, *Philodromus vulgaris* (Hentz 1847) (Philodromidae) and *Metacyrba undata* (De Geer 1867) (Salticidae) in a small woodland, and discovered unexpectedly high levels of infestation. In the spring we collected other types of spiders for comparison and discovered a second species of mantispid, *Climaciella brunnea* (Say 1824), aboard many of them. Because until that time no data had yet been reported documenting more than one mantispid species from the same study site, we continued our collections to see if there was any pattern to the kinds of spiders boarded. It became apparent that these two mantispids were not boarding the same species of spiders.

METHODS

Mantispids are associated primarily with hunting spiders (Redborg & MacLeod 1985; Hoffman & Brushwein 1989, 1990; Redborg 1998). We collected cursorial spiders from

four microhabitats in a four-hectare, oak-hickory forest near Mahomet, Illinois known as Stidham Woods.

Spiders were collected from (1) beneath tree bark during the winter, (2) on shrub-level foliage during the early spring, (3) from the woodland leaf litter during the late spring, summer, and early fall, and (4) from grassy fields bordering the woods during the late summer and early fall. Spiders were later anesthetized with CO₂ and examined under a stereo microscope at 18× magnification for the presence of mantispid larvae. Mantispid boarding frequencies on spiders were analyzed using Chi-square or the Fisher Exact Test.

Bark-associated spiders.—Spiders were collected from beneath the bark of eight living shagbark hickories, *Carya ovata* K. Koch, distributed throughout the entire woods, between 18 December 1982 and 5 February 1983. Loose bark was removed from the trunk up to a height of 4 m. A white sheet was placed around the base of each tree to catch any spiders that fell from the bark.

Between 12 June 1983 and 22 June 1983 additional shagbark hickories were examined for the presence of female spiders guarding egg sacs. Bark was pulled back and the undersurface of it examined. Egg sacs and associated spiders were collected, brought into the laboratory, and the presence of mantispid cocoons and emergence of any adult mantispids were recorded.

Low-level foliage spiders.—Spiders were located on the branches of small trees and shrubs with the aid of a headlamp and collected by hand on 16 May 1983, 19 May 1983 and 21 May 1983.

Leaf litter lycosids.—Wolf spiders (Lycosidae) were collected by hand on three nights in late spring between 21–28 May 1983 from the leaf litter within the woods at night aided by eye reflections from a headlamp. A second sample was taken in mid summer on 30 June. A third sample was taken in the fall on 19 & 26 September 1983.

Egg sacs were obtained from, or collected with, some of these spiders. Spiders and egg sacs were maintained under ambient temperature and photoperiod on a screened porch.

Field lycosids.—Wolf spiders were collected from the grassy field to the north of the woods using a headlamp as described above

on seven nights between 3 August–26 September 1983.

Adult *Climaciella* observations.—Since *Climaciella* adults are known to frequent flowers, the field area to the east and north of the woods was surveyed approximately once a week from 1 July 1983 to 4 September 1983 for the presence of *Climaciella* adults on flowers. This time frame was chosen based on our collection of *Schizocosa* adults with egg sacs in late June (see results).

Voucher specimens of this study are deposited in the Field Museum of Natural History.

RESULTS

Bark-associated spiders.—Most of the spiders collected belonged to two species, *Philodromus vulgaris* and *Metacryba undata* (Table 1). *Philodromus* sits loose beneath the bark and does not produce any type of silken retreat. Some of these spiders were concealed in cracks or crevices while others, aided by their flattened morphology, simply sat adhered to the under surface of the outer bark or the outer surface of the inner layers. Many spiders fell from the tree when the bark was removed and were recovered from the sheet. Specimens of *M. undata* were all contained within dense silken retreats. *Cheiracanthium mildei* (Clubionidae), *Ariadna bicolor* (Segestriidae) and *Herpyllus ecclisiastica* (Gnaphosidae) occupied silk retreats less dense than those of *M. undata*.

Spiders carrying mantispid larvae were collected from all eight trees examined. A high frequency of 64 out of 85 *P. vulgaris* (29 subadult ♀, 30 subadult ♂, 5 juveniles) had been boarded by at least one larva of *M. uhleri*. Eight of these spiders carried more than one larva (seven with two, one with three), most of which (68 out of 73) were tightly adhered to the dorsal, ventral, or lateral surface of the pedicel. Although larvae will enter the book lungs of sufficiently large species of spiders (Redborg & MacLeod 1985), none were found in this area on *Philodromus*. The remaining larvae were located at various positions around the leg bases or underneath the edge of the carapace.

Mantispa uhleri larvae were also found aboard the salticid *Metacryba undata* although its infestation frequency of 25 out of 85 (26%) was significantly lower ($\chi^2 = 43.19$, $P < 0.001$) than the frequency of 64 out of 98

Table 1.—Collections of cursorial spiders from four microhabitats in Stidham Woods, Illinois during 1982–83. (* = May collection; ** = June collection; *** = September collection.)

Micro-habitat	Species	No. of					Total
		No. of juven-iles	No. of adult fe-males	No. of sub-adult males	No. of adult fe-males	No. of adult males	
bark	<i>Philodromus vulgaris</i> (Hentz 1847)	9	36	40			85
bark	<i>Metacyrba undata</i> (De Geer 1867)	68			18	12	98
bark	<i>Cheiracanthium mildei</i> C. L. Koch 1864	1	1				2
bark	<i>Ariadna bicolor</i> (Hentz 1842)	10					10
bark	<i>Herpyllus ecclisiastica</i> Hentz 1832	6					6
foliage	<i>Aysha gracilis</i> (Hentz 1847)	1			6	4	11
foliage	<i>Anyphaena fraterna</i> (Banks 1896)	1			19	18	38
litter*	<i>Schizocosa saltatrix</i> (Hentz 1844)				1		1
litter*	<i>Schizocosa ocreata</i> (Hentz 1844)				4	6	10
litter*	<i>Schizocosa rovneri</i> Uetz and Dondale 1979				1		1
litter*	<i>Schizocosa</i> sp.		55	53			108
litter**	<i>Schizocosa saltatrix</i>				1		1
litter**	<i>Schizocosa ocreata</i>					1	1
litter**	<i>Schizocosa ocreata/rovneri</i>				12		12
litter**	<i>Schizocosa</i> sp.		4				4
litter***	<i>Schizocosa</i> sp.	40					40
field	<i>Rabidosa punctulata</i> (Hentz 1844)	38	19	23	59	46	185
field	<i>Rabidosa rabida</i> (Walckenaer 1837)				5	1	6
field	<i>Hogna carolinensis</i> (Walckenaer 1837)	2					2

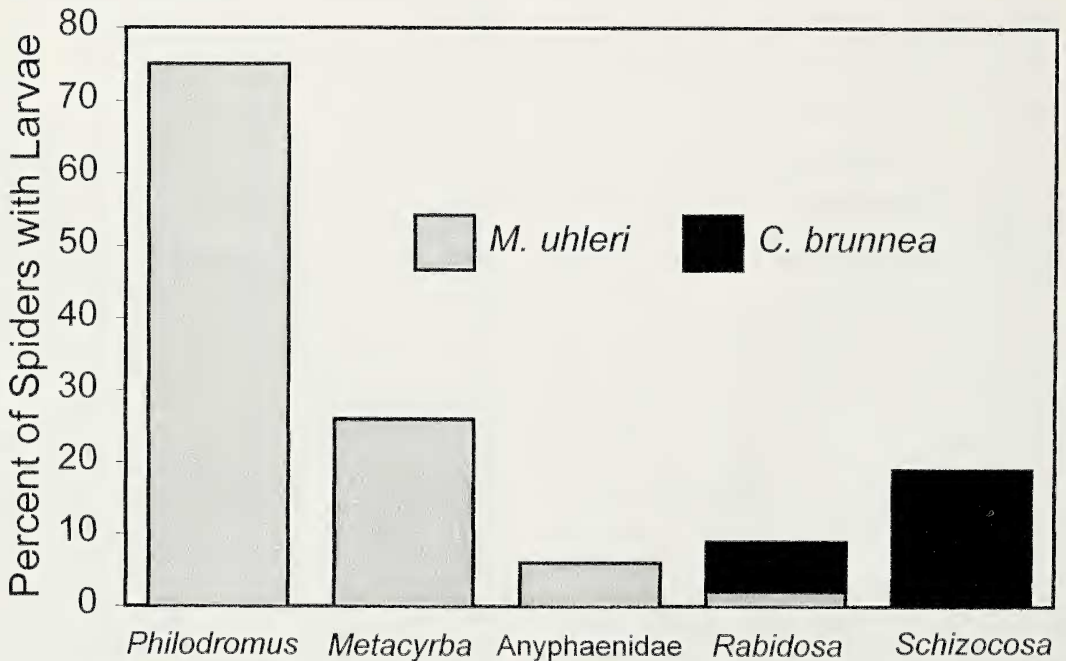


Figure 1.—Percentages of five groups of spiders boarded by first instar larvae of *Mantispa uhleri* and *Climaciella brunnea* (Neuroptera: Mantispidae) from an Illinois woodland. Collections of *Aysha gracilis* and *Anyphaena fraterna* were pooled and are designated Anyphaenidae.

(75%) on *P. vulgaris*. Twenty-five *M. undata* (5 adult ♀, 6 adult ♂, 14 juveniles) had been boarded by at least one larva of the mantispid and two of these spiders carried two larvae each. Most larvae were located on the dorsal, ventral, or lateral pedicel while no larvae occupied the book lungs. One additional bark-associated spider was found boarded by a larva of *M. uhleri*. A subadult female *Cheiracanthium mildei* carried a larva in the right book lung.

***Philodromus* egg sac collections.**—Five female *P. vulgaris* guarding egg sacs were collected on 12 June 1983, 13 were collected on 16 June 1983, and eight were collected on 22 June 1983 for a total of 26 spiders. With the exception of one spider collected on 12 June, all spiders were guarding two egg sacs. In all cases, egg sacs were located on the inner surface of the removed piece of bark. The two sacs were close enough together so that the legs of the spider came in contact with both. The sequence of the two sacs was easy to determine by the differing developmental state of the eggs within and the second egg sac constructed was always the smaller of the two.

Eight of the 26 spiders were guarding sacs that contained a larva or cocoon of *M. uhleri*. The egg sac attacked was always the larger, first sac. Adult mantispids emerged from these sacs on 29 June, 30 June (4 mantispids), 2 July (2 mantispids), and 3 July 1983. Six of the spiders also had egg sacs containing wasp larvae, although which sac was involved varied. One or more wasps emerged from four of the older, first sacs. Wasps were in both of one spider's egg sacs, and one spider that had a mantispid in its first sac had a wasp in the second. Although 75% of overwintering *P. vulgaris* had been boarded by *M. uhleri* larvae, only 31% of the spring egg sacs contained larvae. The frequencies associated with these two percentages are significantly different ($\chi^2 = 15.4$, $P < 0.001$).

Low-level foliage spiders.—All of the spiders collected from this microhabitat were anyphaenids belonging to two species (Table 1). The overall infestation level of *M. uhleri* on Anyphaenids was 6% (3 out of 49). Three *A. gracilis* (1 ♀, 2 ♂) out of 11 carried a larva of *M. uhleri* with two of these larvae on the pedicel and one in a book lung. No larvae were found aboard the 38 *A. fraterna*. The frequencies of *M. uhleri* on these two anyphaenid spe-

cies were significantly different (Fisher Exact Test, $P = 0.009$). The infestation frequency of 3 out of 11 (27%) on *A. gracilis*, however, was no different ($\chi^2 = 0.06$, $P > 0.05$) from that on *M. undata* but was significantly less ($\chi^2 = 8.50$, $P < 0.01$) than that on *P. vulgaris*.

A single larva of *M. pulchella* was also found associated with one of these anyphaenids. It unfortunately was dislodged from its host spider and found loose in the examination chamber with representatives of both spider species so that its exact host association could not be determined.

Leaf litter lycosids.—A total of 120 spiders was collected in May with a second smaller sample of 18 spiders collected in late June (Table 1). Only adult spiders could be reliably identified to species. *Schizocosa ocreata* and *S. rovneri* are sibling species whose males can easily be distinguished by the tufts of black bristles on leg 1 of *S. ocreata* but whose females are morphologically identical (Uetz & Dondale 1979). Some of these females were reliably identified by successfully mating them with a male of the appropriate species. If adult females could not be so mated, they are referred to as *S. ocreata/rovneri* as they could have been either species.

Twenty-three of the 120 (19%) spiders (3 ♀ *S. ocreata*, 1 ♂ *S. ocreata*, 11 subadult ♀ *Schizocosa* sp., 8 subadult ♂ *Schizocosa* sp.) collected at the end of May 1983 had been boarded by at least one larva of *C. brunnea*. Two of these spiders (1 ♀ *S. ocreata* and 1 subadult ♀ *Schizocosa* sp.) carried two larvae. Unlike larvae of *M. uhleri*, which are usually tightly adhered to the pedicel, these larvae were located along the edge of the carapace with their heads oriented toward the pedicel or toward the membranous area between the edge of the carapace and the coxae. Larvae of *M. uhleri* show no visible movement while attached to the pedicel, but larvae of *Climaciella* could be seen to periodically move along the carapace and they could often be seen to seemingly push their mouthparts into the soft areas beneath it. Small drops of what appeared to be spider hemolymph could sometimes be seen adjacent to larval mouthparts or in areas where larvae had recently been.

Of the 18 spiders collected late June, four (2 ♀ *Schizocosa* sp., 2 subadult ♀ *Schizocosa* sp.) carried a larva of *C. brunnea*. One of the adult females produced an egg sac on 3 July

Table 2.—Levels of *Mantispa uhleri* and *Climaciella brunnea* (Mantispidae) aboard the spider *Rabidosa punctulata* (Lycosidae) collected from grassy fields north of Stidham Woods, Illinois in 1983 (* one spider boarded by both mantispid species).

Date	No. of spiders				No. of mantispids	
	Juveniles	Subadults	Adults	Total	<i>M. uhleri</i>	<i>C. brunnea</i>
Aug. 3, 4	34	0	0	34	1*	1*
Aug. 18	2	38	0	40	2	4
Aug. 31	1	4	35	40	1	3
Sept. 19, 21	1	0	32	33	0	2
Sept. 26	0	0	38	38	0	3
Total	38	42	105	185	4	13

1983. On 23 July 1983 an adult male *C. brunnea* emerged from this sac. Three of the adult female spiders not carrying a mantispid larva had an egg sac when collected. Spiderlings emerged from these egg sacs on 7 July, 11 July, and 17 July 1983.

Seven of the 40 juvenile *Schizocosa* collected in September (Table 1), presumably the offspring from July egg sacs, carried a single larva of *C. brunnea*.

The three *Schizocosa* samples yielded no larvae of *M. uhleri*. The frequencies of *Climaciella* infestation were 19%, 22%, and 18%, respectively. They were not significantly different ($\chi^2 = 0.18$, $P > 0.05$) from each other.

Field lycosids.—Collections were predominated by *Rabidosa punctulata* (Table 1). This species overwinters as an adult and produces egg sacs in the spring. Consistent with this scenario, juveniles were collected in early August, subadults in mid-August, and adults in late August and September.

In contrast to the other spiders in this study, *R. punctulata* was boarded by larvae of both *M. uhleri* and *C. brunnea* (Table 2). In fact, one of these spiders carried a larva of both mantispid species. All of the other boarded spiders carried only a single larva. Of the 185 *R. punctulata* collected, four (2%) had been boarded by *M. uhleri* while 13 (7%) had been boarded by *C. brunnea*. Although the frequency of *C. brunnea* on *R. punctulata* was significantly greater than that of *M. uhleri* ($\chi^2 = 3.95$, $P < 0.05$), there were significantly more *C. brunnea* on *Schizocosa* in May ($\chi^2 = 9.17$, $P < 0.005$). No mantispids were found on either *R. rabida* or *H. carolinensis*.

Adult *Climaciella* collections.—The fields

to the north and west of the woods were surveyed for adult mantispids on flowering plants approximately weekly on 10 dates in July, August and September. In July, the most conspicuous plants in bloom included red clover, *Trifolium pratense* L.; wild carrot, *Daucus carota* L.; ox-eye daisy, *Chrysanthemum leucanthemum* L.; and common milkweed, *Asclepias syriaca* L. These were followed in August by thistle, *Cirsium* spp. and sunflower, *Helianthus* spp. and, in September, goldenrod, *Solidago* spp. The only mantispids found on these plants were five *C. brunnea*. Three females were observed on three different milkweed plants on 17 July. A courting male was found associated with one of these females. The male's behavior was similar to that described by Boyden (1983) for *C. brunnea* on milkweed in Minnesota. A sweet musk-like odor, presumably pheromone, from this male was quite apparent. A fourth female was observed, also on milkweed, a week later on 23 July.

DISCUSSION

It was actually more difficult to find a specimen of *P. vulgaris* from Stidham Woods not carrying a mantispid than it was to find one that did. While the exceedingly high levels of both *M. uhleri* and *C. brunnea* at this field site may seem excessive to some, we contend this is not an anomaly. An ongoing study of the distribution of mantispids in Iowa has so far involved the collection of over 5000 specimens of *P. vulgaris* and *M. undata* and, in areas in eastern Iowa where *M. uhleri* occurs, its levels on *P. vulgaris* range from 16–70% and on *M. undata* range from 8–33% (unpubl. data). Thus, while the levels of 75% and 26%

reported here are high, they are not incongruous and certainly comparable to levels found in Iowa. Scheffer (1992) recently reported associations between *Climaciella* and *Schizocosa* from Cincinnati and northern Kentucky. Although she did not report frequencies, her report does not suggest that spiders bearing *Climaciella* larvae were difficult to find.

Up to now, most mantispid studies have dealt with single species and have focused primarily on the documentation of spider hosts. Data are now needed involving sympatric species of mantispids collected from an area small enough to make some meaningful comparisons regarding resource partitioning. A recent study reports two Japanese mantispids boarding two different groups of spiders in deciduous forests (Hirata et al. 1995). Larvae of *Mantispa japonica* were found on spiders collected on plants while *Eumantispa harmandi* were found aboard spiders associated with the forest floor. However, no levels of infestation were reported and no statistical comparisons made.

Both *M. uhleri* and *C. brunnea* are spider boarders that overwinter on their respective host spiders and enter egg sacs when they are constructed the following year. Although *M. uhleri* will board a wide variety of hunting spiders, it is becoming increasingly apparent that *P. vulgaris* is its major host in much of the North American Midwest. Larvae of *M. uhleri* enter *P. vulgaris* egg sacs in May and June and emerge as adults in late June and early July. Newly-hatched *M. uhleri* larvae should begin appearing in mid-to-late July.

While the spider *M. undata* is also an important host for *M. uhleri*, its role pales in comparison to that of *P. vulgaris*. Hoffman & Brushwein (1989) hypothesized that *M. pulchella*'s greater association with anyphaenids, salticids, and clubionids as opposed to philodromids, oxyopids, and thomisids was due to the fact that the former spiders make silken retreats that perhaps enabled larvae to locate or board them more easily. There is no evidence for this in *M. uhleri* because *P. vulgaris* lacks retreats. Also, the flattened resting posture of *Philodromus* would allow much leg and venter surface area to contact the substrate, thus facilitating larval contact.

Both spider groups reported here (*Schizocosa* and *Rabidosa*) as hosts for *C. brunnea* are the same as those reported by Redborg &

MacLeod (1983) in southern Illinois. Of the two host groups, the most important appears to be members of the genus *Schizocosa*. The infestation level of 19% on the nearly mature *Schizocosa* collected in May represents larvae that likely had overwintered on these spiders. Our collecting data suggest that egg sacs from *Schizocosa* probably are produced in late June and early July. The emergence of the *C. brunnea* adult on 23 July from the egg sac of a *Schizocosa* collected 30 June corresponds with the appearance of adults on milkweed in the field. One might therefore expect newly-hatched *Climaciella* larvae to begin appearing in late July or early August. These would be the larvae that were then found on the juvenile *Schizocosa* in September. The almost identical level of 18% infestation on these spiders compared to those collected in May suggests that *Climaciella* population levels were fairly stable.

Within the wooded area, there was absolutely no overlap of host range between *M. uhleri* and *C. brunnea*. The division of spider resources seems to be based on vertical stratification. All of the spiders associated with *M. uhleri* are foliage-inhabiting spiders while the main host for *C. brunnea*, *Schizocosa*, is usually confined to the forest floor. One could argue that this differential association is due to restricted host preferences on the part of the larvae, but we think it more likely due to differences in adult ovipositional or larval searching behavior. *Mantispa uhleri* will readily board lycosids under laboratory conditions and has been found at various times on virtually every group of hunting spiders including species of *Schizocosa* in southern Illinois (Redborg & MacLeod 1985), and *Climaciella* will board spiders other than lycosids in the laboratory (Redborg & MacLeod 1983). While it is true that all of the associations in this report, as well as all other published data, link *Climaciella* with lycosids, we think this can best be explained by behavioral factors which keep *Climaciella* larvae close to the ground.

Although there is currently no direct evidence documenting ovipositional sites for *M. uhleri* in the field, its high levels on *Philodromus* suggest that this mantispid may be laying its eggs in the foliage or branches of the forest canopy. Our observations through the years suggest to us that *P. vulgaris* develops

in the tree canopy. For instance, each October, following the first frost, appreciable numbers of subadult *Philodromus* can be found collecting between the window frames and sills of the science building on the Coe College campus. These spiders are not evident during the summer on the walls of the building and there is no significant low-lying vegetation surrounding the building other than the frequently-mowed lawn. It seems reasonable that the spiders have been developing on the foliage or branches of the several oaks that line the grounds around the building. We regard the window sills and frames of the building as being the "urban" ecological equivalent of loose bark. Published data concerning the life history of this spider are crucially needed.

In contrast, we suggest that *C. brunnea* adults, although they may aggregate, mate and feed on nearby flowers, enter the woods and lay their eggs on or near the ground. *Climaciella* larvae do not actively search as do the larvae of *M. uhleri* but instead adopt a phoretic posture in which they rear up on their tails and sway back and forth with legs outstretched (Redborg & MacLeod 1983). It is thus not likely that larvae will travel a great distance from their egg clutch. Their strategy as obligate spider boarders is to wait for spiders to come to them. They would be most likely to come in contact with active spiders which certainly characterizes the Lycosidae. To produce infestation levels of 19% on *Schizocosa*, that waiting place, and by extension the site of adult oviposition, is most probably on or near the ground.

In light of these arguments, the occurrence of larvae of both species of mantispids on *R. punctulata* in the field adjacent to the woods is corroborative. The vegetation here has limited vertical stratification of no more than a few feet. Mantispids of either species that attempted to oviposit in the field would wind up laying eggs in basically the same area—on the ground, on various grasses, or on the foliage of low-lying plants. The salt marsh in southern Mississippi studied by LaSalle (1986) would have been structurally somewhat reminiscent of the area studied here. He found *Climaciella* there laying eggs at the tips of leaf spikes of *Juncus* rushes. We can imagine similar ovipositional behavior here for both *M. uhleri* and *C. brunnea*. *Rabidosa punctulata*, along with its sibling species *R. rabida*,

is usually found in grassy areas. Spiders were collected both on the ground and crawling along the foliage of grasses and other plants. Thus, whatever vertical stratification is present is probably completely traversed by this spider. And this, appropriately enough, is the one place where there is overlap of host range. We found larvae of both species on this spider. In fact, one spider carried a larva of both *M. uhleri* and *C. brunnea*. This is, to our knowledge, the first documentation of two different species of mantispid aboard the same spider.

It is important to note that the 2% infestation level of *M. uhleri* and the 7% level of *C. brunnea* on *R. punctulata* are both significantly lower than their respective levels on other spiders, suggesting that the field area is not the preferred ovipositional location for either species. Also strongly supported is the contention that *C. brunnea* is leaving its flower-inhabiting aggregation areas to lay its eggs within the woods. If adults were preferentially laying their eggs near their mating sites on milkweed, one would expect to find significantly more larvae on *R. punctulata* than *Schizocosa*. Just the opposite is true. The significantly higher level of *C. brunnea* on *R. punctulata* compared to that of *M. uhleri* is consistent with the sit-and-wait specialization of this mantispid that may favor the selection of lycosids as hosts. Although neither parasite favored the grassy field area for oviposition, *C. brunnea* may wind up laying more eggs there because of the necessity to travel between the two sites.

While the infestation level of *M. uhleri* on *R. punctulata* is slight, the infestation level of *C. brunnea* on this spider is more substantial. There is the potential for a complex, overlapping life cycle similar to those described for *M. uhleri* (Redborg & MacLeod 1985) and *M. pulchella* (Hoffman & Brushwein 1989). *Rabidosa punctulata* females overwinter as adults and produce egg sacs early in the spring. Larvae that survived the winter on this spider would probably have emerged from egg sacs before we looked for adults in the summer. *Climaciella* offspring might appear early enough in the year to board *Schizocosa* spiders destined to spin egg sacs that same summer, or they might board immature *R. punctulata* that would not spin sacs until the following year. One or two generations per year are thus possible. Future study will be

necessary to assess the importance of this spider in the population dynamics of *C. brunnea* and vice-versa.

The finding of a single larva of *M. pulchella* on one of the anyphaenids in this study is intriguing. It is consistent with the findings of Hoffman & Brushwein (1989) who found *M. pulchella* in South Carolina associated with small foliage-inhabiting wandering spiders. In fact, anyphaenids yielded the greatest number of *M. pulchella* larvae in their study with both *A. fraterna* and *A. gracilis* serving as hosts. More extensive collecting of small wandering spiders might have uncovered additional larvae of *M. pulchella* and the existence of a third level of resource partitioning in Stidham Woods. It is also possible that *M. pulchella* is truly rare here, perhaps unable to compete successfully on its normal hosts due to the high level of competition from *M. uhleri*.

If one focuses on the anyphaenids as a group, the infestation level of *M. uhleri* is only 6%, intermediate between the high levels on *Philodromus/Metacryba* and the non-existent level on *Schizocosa*. However, this may be misleading. All *M. uhleri* associated with this family were aboard *A. gracilis* and none aboard *A. fraterna*. It is possible that these two spiders, although collected from the same microhabitat early in the spring, may be occupying different areas during the critical time when *M. uhleri* larvae are boarding them. Still, Redborg & MacLeod (1985) did find *M. uhleri* aboard *A. fraterna* in southern Illinois. More extensive sampling will be needed to answer this question.

While 75% of overwintering *P. vulgaris* had been boarded by *M. uhleri* larvae, only 8 of 26 (31%) of egg-laying *P. vulgaris* were affected with a larva in their first sac. This significant difference shows that some larval mortality occurs between overwintering and egg sac production. There may be spider behavioral mechanisms that reduce the number of larvae successfully entering egg sacs. Of particular interest here are the two egg sacs spun and guarded by this spider. Mantispid larvae were only found in the larger first egg sac. Eggs in the second egg sac escaped predation, at least by mantispids. This is very high selective pressure which could have shaped the egg-laying strategy of *P. vulgaris*. Recent evidence (Vittitoe 1991) indicates that

the second egg sac of *P. vulgaris* is an anti-mantispid mechanism evolved specifically to thwart *M. uhleri* predation.

The small area of our study site may have affected the way in which these two mantispids interacted here. Perhaps in larger more extensive woods, *C. brunnea* is restricted to the interface between woods and field while *M. uhleri* populations are more homogeneously distributed in woods or even concentrated within the interior. Such spatial differences might be muddled in small woodlands. Thus resource partitioning between these two species may involve additional horizontal components.

We acknowledge that our sample of hunting spiders from Stidham Woods deals with only a small number of species and is thus incomplete, but the four different microhabitats they represent provide a good beginning for understanding the differences between these two mantispids. Future work should focus on additional spider groups, particularly those of the surrounding fields, where greater overlap between *M. uhleri* and *C. brunnea* is predicted.

In 1975 we attended the annual meeting of the American Arachnological Society and one of us (K.E. Redborg) presented some preliminary graduate student research on spider boarding behavior by larval mantispids. Findings suggested that these insects were much more common than had been previously supposed. Following the talk B.J. Kaston commented that, although he found the results interesting, his general impression through the years was that mantispids were "as scarce as hen's teeth." Later, H.W. Levi informed us that he had commonly seen what appeared to be such larvae attached to the pedicel of spiders that he had collected in Wisconsin. A few weeks after the meeting J.E. Carrel wrote that, sparked by our discussions, he had examined a large container of preserved wolf spiders from his lab and discovered a "scum" of mantispid larvae floating on the top. Some textbooks still regard mantispids as being a novel but obscure group of insects, at least in temperate North America. The time has now arrived when these fascinating insects may no longer be regarded as rare but can more properly be assessed as having an important impact on spider ecology and an important role in the evolution of spider behavior.

LITERATURE CITED

- Boyden, T.C. 1983. Mimicry, predation and potential pollination by the mantispid *Climaciella brunnea* var. *instabilis* (Say) (Mantispidae: Neuroptera). J. New York Entomol. Soc., 91:508–511.
- Brushwein, J.R., K.M. Hoffman & J.D. Culin. 1992. Spider (Araneae) taxa associated with *Mantispa viridis* (Neuroptera: Mantispidae). J. Arachnol., 20:153–156.
- Hirata S, M. Ishii & Y. Nishikawa. 1995. First instar larvae of mantispids, *Mantispa japonica* MacLachlan and *Eumantispa harmandi* (Navás) (Neuroptera: Mantispidae), associating with spiders (Araneae). Japanese J. Entomol., 63:673–680.
- Hoffman, K.M. & J.R. Brushwein. 1989. Species of spiders (Araneae) associated with the immature stages of *Mantispa pulchella* Banks (Neuroptera, Mantispidae). J. Arachnol., 17:7–14.
- Hoffman, K.M. & J.R. Brushwein. 1990. Spider (Araneae) taxa associated with the immature stages of *Mantispa interrupta* (Neuroptera: Mantispidae). Entomol. News, 101:23–28.
- LaSalle, M.W. 1986. Note on the mantispid *Climaciella brunnea* (Neuroptera: Mantispidae) in a coastal marsh habitat. Entomol. News, 97:7–10.
- Redborg, K.E. 1998. The biology of the Mantispidae. Ann. Rev. Entomol., 43:175–194.
- Redborg, K.E. & E.G. MacLeod. 1983. *Climaciella brunnea* (Neuroptera: Mantispidae): a mantispid that obligately boards spiders. J. Nat. Hist., 17:63–73.
- Redborg, K.E. & E.G. MacLeod. 1985. The developmental ecology of *Mantispa uhleri* Banks (Neuroptera: Mantispidae). Illinois Biol. Monogr., #53. 130 pp.
- Rice, M.E. 1986. Communal oviposition by *Mantispa fuscicornis* (Say) (Neuroptera: Mantispidae) and subsequent larval parasitism on spiders (Arachnida: Araneida) in south Texas. J. Kansas Entomol. Soc., 59:121–126.
- Rice, M.E. & W.B. Peck. 1991. *Mantispa sayi* (Neuroptera: Mantispidae) parasitism on spiders (Araneae) in Texas, with observations on oviposition and larval survivorship. Ann. Entomol. Soc. America, 84:52–57.
- Scheffer, S.J. 1992. Transfer of a larval mantispid during copulation of its spider host. J. Insect Behav., 5:797–800.
- Uetz, G.W. & C.D. Dondale. 1979. A new wolf spider in the genus *Schizocosa* (Araneae: Lycosidae) from Illinois. J. Arachnol., 7:86–87.
- Vittitoe, D.A. 1991. A possible anti-mantispid (Neuroptera: Mantispidae) behavioral mechanism in the spider *Philodromus vulgaris* (Hentz) (Araneae: Philodromidae). Unpubl. thesis. Coe College; Cedar Rapids, Iowa, USA.

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